

DO SYMBIOTIC PEA CRABS DECREASE GROWTH RATE IN MUSSELS?

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ABSTRACT

Pea crabs living within the mantle cavities of a variety of bivalve hosts have several adverse effects. In blue mussels (*Mytilus edulis* L.), the crab *Pinnotheres maculatus* (Say) steals food strands and causes gill lesions. We studied the long-term stress of *P. maculatus* on its host by measuring shell accretion in the field, and by numerically characterizing shell shape. Shell form in *M. edulis* is presumed to reflect environmental and physiological history. We computed growth increments in infested populations of mussels over a three-month period at two sites with high and low nutrient regimes. When growth was measured by change in shell length, significant differences between mussels with and without large pea crabs occurred at the low nutrient site, but not where mussels enjoyed a high nutrient regime. To integrate very long-term disparity in growth rates associated with infestation, we used mussels from a robust, naturally occurring population. We recorded and analyzed mussel silhouette shapes with a video digitizer. Elliptic Fourier approximation completely characterized the two-dimensional outlines of shells in such a way that the allometric dependence of shape variables on shell size could be easily removed. At this evidently favorable site, infested mussels displayed significant shell shape distortion characteristic of reduced growth rates. Thus, even in apparently benign environments, pea crab infestation appears to be a chronic stress to *M. edulis*.

INTRODUCTION

Pinnotherids, or pea crabs, are a group of decapod crustaceans adapted for life within other marine animals. Two hundred fifty-two species of pinnotherids have been described (Schmitt *et al.*, 1973). In this spectrum of species, there is a gradation from specialist crabs to generalist crabs with regard to host and geographic range. *Pinnotheres maculatus*, the species in this study, can be considered an ultimate generalist, "demonstrating a profound lack of host specificity" (McDermott, 1962). It has a host list of at least 21 species in several bivalve and polychaete families, and is distributed throughout the subarctic, temperate and tropical zones.

Females of *Pinnotheres maculatus* are soft-shelled and live their entire adult lives within the host—in this case the bivalve *Mytilus edulis*. The crab positions itself on the gills and uses its chelae to pick up mucous food strands from the host that pass by. This species of pea crab has "dwarf" males; they rarely exceed 6 mm across the carapace, and are able to move freely from mussel to mussel. Males can feed independently of mussels (Caine, 1975) and therefore may not represent as much of a drain on a host as a female. Small, immature female pea crabs are also able to move from host to host. When a female pea crab is larger than approximately 6 mm across the carapace, it is unable to leave its host easily because the mussel's gape is not large

enough. *P. maculatus* females do not produce eggs until the summer after they reach the first true crab stage (Pearce, 1964). Since the smallest ovigerous females are 6 mm across the carapace, pea crabs of this size must be one or more years old (*cf.* growth curves for *P. osireum* in Christensen and McDermott, 1958). Large pea crabs have presumably remained within their hosts for at least one growing season.

While pea crabs have experimentally detectable effects on several variables measured for bivalve hosts (Haven, 1959; Silas and Alagarwami, 1965; Pearce, 1966; Kruczynski, 1972; Anderson, 1975; Pregonzer, 1979, 1981), their long-term cumulative effect on host physiology is unknown. Pea crabs can live in a host for at least two to three years (Pearce, 1966; manuscript by N. Bourne, Department of Fisheries and Oceans, Pacific Biological Station, Canada, "Pinnotherid crabs in butter clams, *Saxidomus giganteus*: a commensal or parasite"). The energetic demand of supporting a pea crab may impair host response to long or short term stresses, and might therefore be reflected in a variety of parameters.

If the long-term negative effects of pea crab infestation are to be characterized, an integrated record of the host's physiological history is needed. The bivalve shell provides such a record. Rhoads and Pannella (1970) and Pannella and McClintock (1968) demonstrated that "microgrowth" changes due to varying food, temperature, *etc.*, are reflected in the molluscan shell. Seed (1968) and Lewis and Powell (1961) showed that differences in mussel shell shapes vary with age but also with the environmental conditions to which the animals had been subjected. The degree of divergence between the shapes of two mussels of the same age should be related to the time spent under differing conditions. In general, a fast-growing mussel is triangular or "spatulate" because large, even shell increments are added to the posterior of the shell. Slow-growing mussels add smaller and less even shell increments; over time, the shell therefore takes on an elongate and slightly recurved or "ungulate" appearance. These two forms are illustrated in Figure 1A.

We examined the effects of the generalist crab *Pinnotheres maculatus* on shell growth of its bivalve host *Mytilus edulis*. We measured differences in growth rate over the short term with field experiments, and over the long term by an analysis of shell shape using an elliptic Fourier technique (*cf.* Gevirtz, 1976).

MATERIALS AND METHODS

Mussels were collected from a depth of 30 meters off Gay Head, Martha's Vineyard, Massachusetts. To avoid using very young or very old mussels, only those in the length

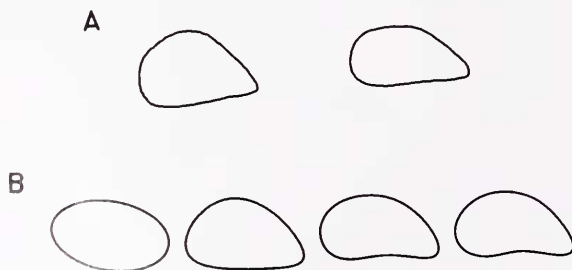


FIGURE 1. Mussel shell shape and its elliptic Fourier decomposition. A. At left, a triangular or "spatulate" mussel shell form characteristic of fast-growing mussels. At right, an elongate and slightly recurved "ungulate" form characteristic of slowly growing animals. B. Successively better approximations of a typical mytilid contour using 1, 2, 3, and then 4 harmonics from an elliptic Fourier decomposition of shell outline.

range of 50.0 to 90.0 mm were used for experimentation. This selection avoids the predictable and extreme effects on shape due to age. Very young animals are known to be spatulate while very old ones become unguulate (Lewis and Powell, 1961). Of mussels from this sample, 199 were dissected immediately to determine the percentage of infestation by pinnotherids.

Field experiment

One hundred twenty animals were engraved with an identification number and were measured to the nearest 0.1 mm with vernier calipers for length (maximum anterior-posterior axis), height (maximum dorso-ventral axis), and width (maximum lateral axis). These mussels were suspended in wide-mesh cages 2 meters above the substrate in two nutritionally different environments off Long Island, New York. These transplants suffered, on average, 12% mortality. After three months (June through August 1980), 100 surviving animals were re-measured and dissected, and the size and sex of each pea crab was recorded. We used analysis of variance to assess the effects of site and pea crab infestation on growth rate as measured by the three morphological dimensions of the host. Infestation levels before and after the experiment were compared using a G-test.

The 'nutrient-rich' environment was in protected harbors of Long Island Sound (Port Jefferson) and the 'nutrient-poor' environment was off the south shore of the island (Shinnecock). Previous work by independent researchers supports this characterization. Newell *et al.* (1982) showed the energy content of available seston averaged $50 \text{ J} \cdot \text{l}^{-1}$ near the first site *versus* $20 \text{ J} \cdot \text{l}^{-1}$ at the second during the summers of 1978 and 1979. Over the last ten years, the nutrient-rich environment has also been about three times higher in levels of phosphate and total inorganic nitrogen (nitrate, nitrite, and ammonia) than the nutrient-poor environment (data supplied by R. Nuzzi and M. Waters, Suffolk County Department of Health, pers. comm.).

Shape analysis

Eighty-two right valves of *Mytilus edulis* were used in a comparative shell shape analysis. These shells were collected from the same biological population at Gay Head, but were not used in the field experiment described above. Thus they form a statistically independent sample of mussels from that population. Using a video camera, we recorded the two-dimensional silhouette of each animal on a bright background. A computer program traced the outline of each valve, which is defined as the locus of points at which brightness changes from dark to light, or light to dark, on vertical or horizontal transects of the image. The details of the technique are discussed by Ferson *et al.* (1985).

We used elliptic Fourier decomposition (Kuhl and Giardina, 1982) to compute coefficients that describe shell shape. This is a very general method that, by treating x-coordinates independently of y-coordinates and by using only the first differences of change in either direction, asymptotically yields a perfect fit to practically any closed curve. We computed the Fourier coefficients for the first four harmonics for each shell. Since x- and y-directions are evaluated separately for sine and cosine terms, there are four coefficients per harmonic. However, three of the 16 coefficients degenerate under normalizations for trace starting point and shell position, size, and rotation. We therefore used 13 nontrivial coefficients. These were more than adequate to describe these simple forms. Figure 1B displays a sequence of improving approximations to a shell outline using 1, 2, 3, and then all 4 harmonics. The coefficients constitute a numerical

decomposition of the shell's entire two-dimensional shape. We averaged these coefficients element-wise to obtain the mean shell form for each group (with and without large crabs). Following Younker and Ehrlich (1977), we used the coefficients as variables in a multivariate test of difference in central tendency between the groups. We used Mahalanobis' D^2 statistic (Mahalanobis, 1936) as a measure of this difference and evaluated its significance with a randomization test (Sokal and Rohlf, 1983, p. 787). Although the Fourier coefficients were arithmetically normalized for scale change (Kuhl and Giardina, 1982), we used a multivariate analysis of covariance with mussel length as the covariate to account statistically for any allometry in shell shape. For purposes of display we also computed the linear discriminant function separating the groups for these Fourier descriptors. This use of the discriminant function is a distribution-free technique (Lachenbruch, 1975).

RESULTS

In the dissected sample, 69% of the mussels contained a pea crab; 31% had females over 6.0 mm, and 38% had smaller females or males. Over the size range 50.0 to 90.0 mm in length, there is no significant correlation between the size of pea crab and the size of mussel host ($P > 0.2$; $R^2 = 0.04$). Figure 2 displays the scattergram.

Field experiment

Following the three-month field experiment, thirty-nine out of 100 surviving mussels harbored a pea crab of any size. Thirty-five (or 90%) of these had a mature female crab. Thus, the infestation level by small pea crabs, which had been 38% in the immediately dissected sample, dropped to 4% over three months in a population of suspended hosts. The difference between these frequencies is significant at the $P < 0.001$ level by a goodness of fit G-test using Williams' correction (Sokal and Rohlf, 1983, p. 704). Since crabs can live two to three years (Christensen and McDermott, 1958), normal mortality does not account for this reduction. However, since crabs attempting to change hosts would likely be lost from the sample by falling to the substrate, a high frequency of host-switching would account for reduced infestation by small crabs. In any case, one can infer that only large female pea crabs remain within their hosts over long periods of time.

Using original shell length as the covariate, we did a multivariate analysis of covariance on measured increments for the three shell dimensions after the short-term growth experiment. The average values are displayed in Table I. The mancova detected no significant differences in growth increment across the size range of mussels used. Thus the narrowness of this range seems to have controlled for allometric dependence of growth on size. Under Wilk's criterion (Rao, 1973, p. 555), we observed a highly significant effect due to site ($F = 6.59$; $P < 0.0005$). The mussels growing in the environment that we had designated as 'high-nutrient' grew substantially more, especially in the length dimension, than mussels growing in the 'low-nutrient' environment. We take this result as biological confirmation of the expectation based on chemical and energetic analyses of nutrient levels in these environments.

The analysis also detected a significant effect on growth increment due to infestation by large pea crabs ($F = 2.91$; $P < 0.038$). Since the bulk of this effect was contained in the length increment, we did a (univariate) two-way analysis of variance to explore this difference. In this closer look, however, we observed an interesting and significant interaction between pea crab infestation and site effects. In particular, there was little change in mussel growth increment due to pea crabs at the high-nutrient environment,

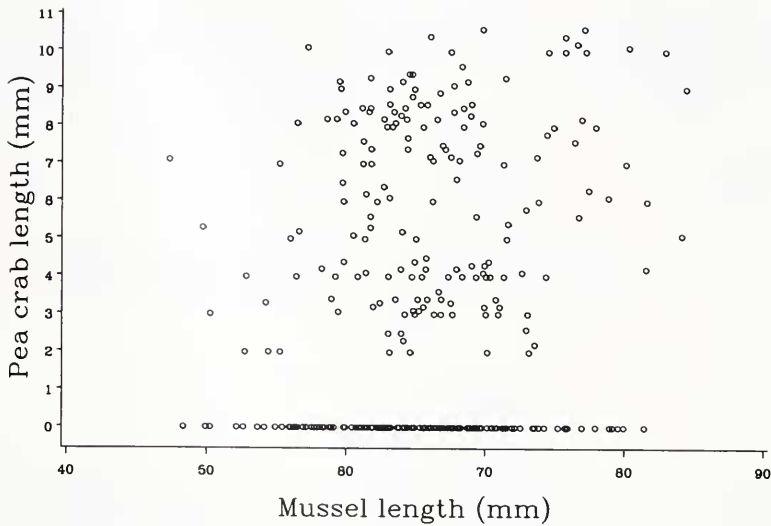


FIGURE 2. Symbiont pea crab carapace length as a function of host mussel shell length. This relation seems to be governed only by gross physical constraints on the largest crab a mussel of a given size can harbor. For the mussel size range of 50 to 90 mm, the regression is not statistically significant.

while at the nutrient-poor environment, the presence of an adult female crab (≥ 6.0 mm) resulted in a significantly lower growth increment in length ($P < 0.01$). Figure 3 shows this variation between the two nutrient regimes. In no cases were there detectable (univariate) width or height differences attributable to the presence of pea crabs.

Shape analysis

Using the 13 elliptic Fourier coefficients as shape descriptors, we computed the mean shell shapes for mussels with and without large pea crabs. Mahalanobis' generalized distance D^2 between the multivariate means of these two groups is 2.62; the probability of observing such a large value by chance alone was estimated in a randomization test involving 370 trials to be lower than 0.005. Thus, even though they are probably indistinguishable to a casual human observer, the shell shapes are statistically significantly different between the two groups.

A more conservative test for difference in shell shape between groups with and without pea crabs is a multivariate analysis of covariance that accounts for allometry of shape with mussel size. We performed a mancova on these two classes of shells with length as the covariate and the 13 shape coefficients as the dependent variables. For Wilk's criterion, we observed an F-value of 2.61 for an overall effect of classification with respect to the presence or absence of a large pea crab. This value is significant $P = 0.005$. We therefore conclude that the presence of a pea crab is associated with a change in shell shape. The overall shell length effect is not significant ($F = 0.99$; $P > 0.47$). Apparently, the arithmetic normalization for the size of shell made in the elliptic Fourier analysis removed any statistically detectable allometry from the shape variables.

Figure 4 displays the mussel shapes distributed along the major discriminant axis. This arrangement shows that unguulate mussels indeed separate from spatulate ones

TABLE I

Sample size, measurements (in length, width and height) and initial shell length for classes of mussels

	N	Length	Δl	Δw	Δh
<i>Pea crab</i>					
with	40	65.3	2.5	.4	.6
without	60	65.6	3.0	.4	.7
***Site					
good	72	66.0	2.9	.4	.6
poor	28	64.2	2.4	.2	.7
Total	100	65.4	2.8	.4	.7

Units are millimeters. Asterisks indicate the level of significance for the factor.

along the direction that, in a linear sense, best distinguishes mussels that harbor pea crabs from those that do not. This pattern corresponds to the expectation derived from Seed (1968) under the assumption that harboring a pea crab is in fact associated with a reduced growth rate.

DISCUSSION

The nature of the host-crab relationship has been the subject of much speculation in the scientific literature for over forty years. Most evidence to date implies that the pea crab is not the desirable "guardian of the Pinna" as Aristotle claimed (see Thompson, 1910, p. 547b), but is more of a parasite than a commensal. Gill lesions, found in infested *Mytilus edulis* (McDermott, 1962) and *Crassostrea virginica* (Flower and McDermott, 1952; Christensen and McDermott, 1958; Haven, 1958), were attributed to the crab's scraping its chelipeds across the host's soft body parts while feeding. Pearce (1966) mentioned an indentation in the gonadal mass of a variety of host clams and mussels. Fibrous lumps or nodules, up to one centimeter in length, have been found on the mantle lips of bivalves harboring pea crabs (Stauber, 1945; Dix, 1973; Jones, 1977). Kruczynski (1972) noted a reduction in dry meat weight of infested scallops when compared with uninfested scallops of the same size. Bivalve meat reduction was greater than the amount corresponding to the physical mass of the pinnotherid. Similarly lowered meat contents were reported for oysters (*C. virginica*) containing *P. ostreum*, and the California mussel (*M. californianus*) containing *Fabia subquadrata* by Haven (1958) and Anderson (1975), respectively. Notched scallops containing pea crabs grew less over a three-month period than uninfested *Argopecten irradians* of similar size. Kruczynski (1975) proved that *Pinnotheres maculatus* ingests the food of *Mytilus edulis* by observing accumulation of ^{14}C in pinnotherid tissue after the host was fed labeled diatoms (*Nitzschia closterium* and *Thalassiosira pseudonana*). Pregonzer (1979) demonstrated that particles of neutral red dye are cleared from water at a slower rate by mussels that contain pea crabs (*Pinnotheres hickmani*). Silas and Alagarwami (1965) reported that a hermaphroditic species of Indian oysters (*Ostrea cucullata*) normally exhibiting a 50:50 sex ratio becomes significantly skewed toward maleness when infested with pinnotherids. They suggested that the stress on the host allows only sperm production instead of energetically more expensive egg production.

Some researchers have reported that size of pea crab is related to size of the host [e.g., Wells (1940) on *Fabia subquadrata* in the mussel *Modiolus modiolus*, and Lopez (1982) on *Pinnotheres modiolicola* in the mussel *Modiolus metcalfei*]. We calculated

Relative frequencies of growth increments for shell length

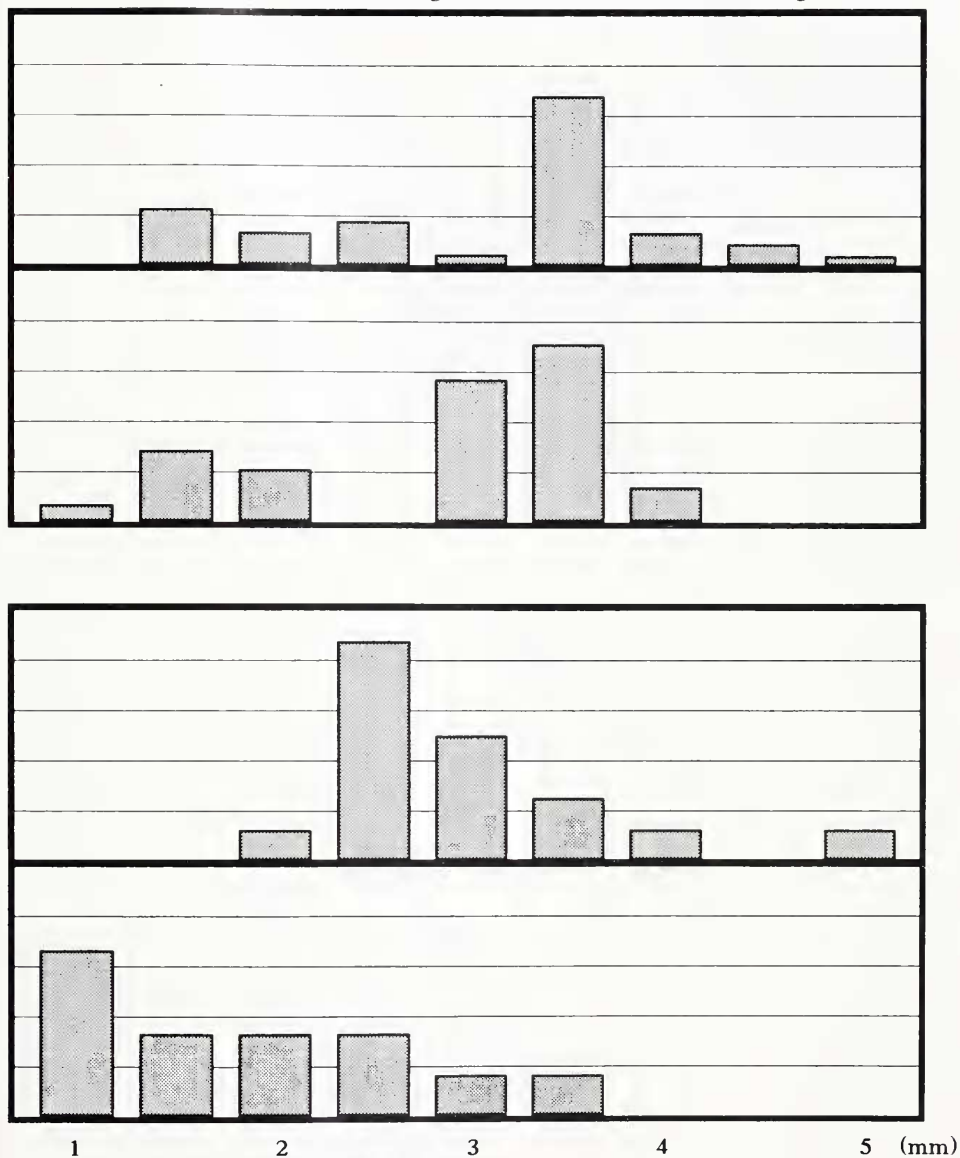


FIGURE 3. Length increment frequencies for mussels in two environments without and with infesting pea crabs. From the top panel, high-nutrient environment without large pea crabs, high-nutrient environment with crabs, low-nutrient environment without crabs, and low-nutrient environment with crabs. Under high-nutrient conditions, there was no significant difference in growth increment between infested and unfested mussels. In low-nutrient conditions, mussels with large pea crabs grew less over a three-month period when measured by change in shell length.

regression lines for several independent populations and found that, if the smallest mussels containing pea crabs are excluded, there is no significant relationship between size of mussel and size of pea crab. Because small mussels can physically house only small crabs, including them in the regression calculation rotates the best fit line toward

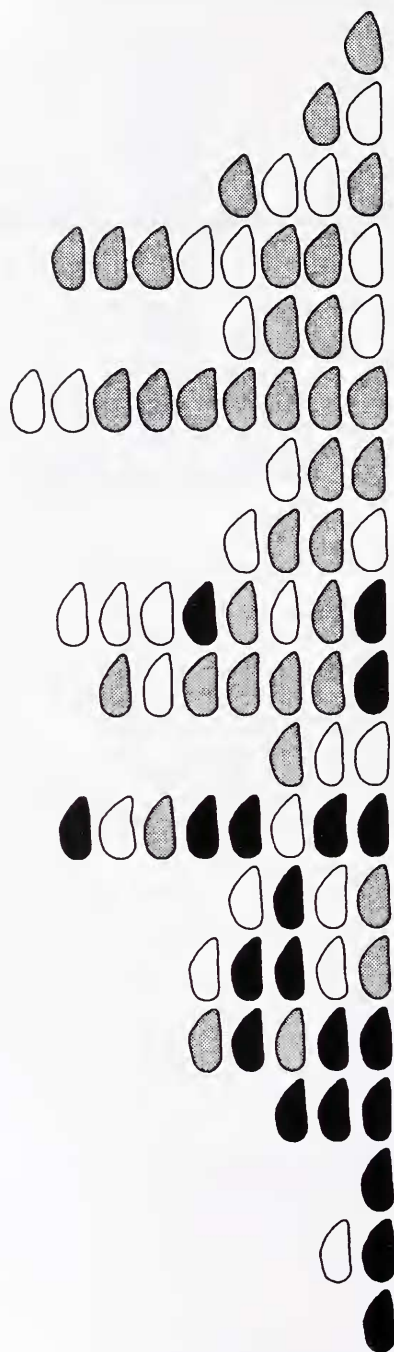


FIGURE 4. The original shell outlines arrayed as a histogram along the linear discriminant axis between shells with and without large pea crabs. Black shells had pea crabs over 6 mm; gray shells had smaller infesting crabs; white shells had no crabs at all. Large crabs are presumably a full year older than small ones and thus have had a chance to influence shell shape in their hosts. Under elliptic Fourier analysis, shells from mussels harboring large pea crabs are significantly different in shape from other mussels. Since these (black) mussels are more elongate, the direction of this shape difference is consistent with the hypothesis that pea crab infestation retards mussel growth.

the origin. Although the regression becomes significant, only 4% of the variation is explained. In the size range of 50 to 90 mm, there is no trend for large *P. maculatus* to be found in larger *M. edulis*.

Our short-term field study indicates that the mere presence/absence of a pea crab may not be the appropriate criterion by which to divide host groups when investigating deleterious effects of pinnotherids. Male and small female pea crabs are not really 'present' over long periods because they can and do move freely from host to host. The fact that a potential host is empty when an experimenter opens it provides no information about the recent past. A large pea crab may have recently died, or a small pea crab may have just moved out. Fortunately, we were able to quantify the frequency of small crab host-switching by suspending infested mussels in a wide mesh cage 2 meters above the substrate. If a pea crab attempts to migrate under these conditions it falls to the ocean bottom and is lost from the population. While a host on the bottom could easily be re-entered, a pea crab cannot readily return to suspended hosts. Work by Pregoner (1981) corroborates our findings. He artificially implanted *P. hickmani* in a raft population of *M. edulis* and, after 4 months, found 46% of the female pea crabs and 100% of the male pea crabs had vacated their hosts. Unfortunately, he does not report the sizes of female pea crabs either lost or remaining. In our experiment, mussels lost 44% of the total number of crabs present, and 90% of the small (< 6 mm) crabs. Based on this information, we maintain that to isolate long-term effects of pea crabs on host physiology, only adult females should be considered as 'infesting.' The short-term effects of small pea crabs on elastic physiological responses in the host (e.g., oxygen consumption, feeding rate, byssal thread production) remain of interest.

In a three-month experiment, mussels both with and without symbiont pea crabs were grown under two nutrient regimes. Under high-nutrient conditions, there were no statistically significant effects on growth increment due to pea crab infestation for length, width, or height of the mussel host. However, under lower-nutrient conditions, length increment was significantly reduced among mussels harboring large pea crabs compared to their uninfested neighbors. Therefore, in stressful environments, two mussels of the same age would not be the same size if one has been harboring a large pea crab.

External morphology in mussels is known to depend on growth rate. A slowly growing mussel records its growth history in the elongate and recurved or "ungulate" shape of its shell. A fast-growing mussel records its history in a triangular or "spatulate" shell shape. Thus shell form represents an integration of physiological status over several years. To examine the long-term effects of harboring a pea crab, we numerically characterized shell shapes for individuals from Gay Head, Massachusetts, that had been infested with at least year-old pea crabs and for individuals that were free of large pea crabs. The bed was an extensive and robust population from which thousands of individuals had been harvested over a two-year period (F. Valois, Marine Biological Laboratory, pers. comm.). Presumably then this was an environment favorable for mussels. In our analysis we corrected for allometry of shape due to size and therefore captured shape itself. By doing so, we were able to differentiate between slightly ungulate mussel shapes characteristic of the presence of large pea crabs, and more spatulate mussel shapes characteristic of uninfested mussels. Thus over the long-term, pea crabs appear to retard host growth rates under conditions that may be only periodically stressing, or even optimal.

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